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Abstract: In alpine environments facilitator species buffer environmental extremes while building up soil resources above that of open areas. These modulating effects are critical for the persistence of species out of their optimal range and contribute to increase community-level plant species richness and phylogenetic diversity. We analyzed the effects of seven potential facilitator species with contrasting morphologies on subordinate plant species along a crossed environmental gradient, linking such effects to canopy effects. We also used these patches consisting of multiple shrub species to evaluate the effects of the whole shrub community on species richness and phylogenetic diversity, and whether such shrub community effects differed along the gradient. We used ecological and phylogenetic data of alpine plant communities along two altitudinal gradients on opposing aspects of the Sierra Nevada Mountains (Spain). As expected, shrubs buffered harsh abiotic conditions by decreasing mean temperatures and increasing relative humidity with regard to open areas. Composition of subordinate plant communities differed among shrubs and among sites, and correlated with relative humidity along the gradient pointing to the dependence of subordinate species on micro-environments created by shrubs. There were a variety of shrub effects on overall plant abundance and richness depending on shrub identity. In the most extreme sites we recorded generally positive effects of the shrub community, which promoted whole-community species richness and phylogenetic diversity despite species-specific effects ranging from clearly negative to positive. Our data therefore show that the effect of different shrub species on plant community richness and phylogenetic diversity is not redundant, as every shrub species may host unique communities, thereby affecting the structure and composition of the whole community.

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Contribution of co-occurring shrub species to community richness and phylogenetic diversity along an environmental gradient.

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Summary

In alpine environments facilitator species buffer environmental extremes while building up soil resources above that of open areas. These modulating effects are critical for the persistence of species out of their optimal range and contribute to increase community-level plant species richness and phylogenetic diversity. We analyzed the effects of seven potential facilitator species with contrasting morphologies on subordinate plant species along a crossed environmental gradient, linking such effects to canopy effects. We also used these patches consisting of multiple shrub species to evaluate the effects of the whole shrub community on species richness and phylogenetic diversity, and whether such shrub community effects differed along the gradient. We used ecological and phylogenetic data of alpine plant communities along two altitudinal gradients on opposing aspects of the Sierra Nevada Mountains (Spain). As expected, shrubs buffered harsh abiotic conditions by decreasing mean temperatures and increasing relative humidity with regard to open areas. Composition of subordinate plant communities differed among shrubs and among sites, and correlated with relative humidity along the gradient pointing to the dependence of subordinate species on micro-environments created by shrubs. There was a variety of shrub effects on overall plant abundance and richness depending on shrub identity. In the most extreme sites we recorded generally positive effects of the shrub community, which promoted whole-community species richness and phylogenetic diversity despite species-specific effects ranging from clearly negative to positive. Our data therefore show that the effect of different shrub species on plant community richness and phylogenetic diversity is not redundant, as every shrub species may host unique communities, thereby affecting the structure and composition of the whole community.

Keywords: community level richness, niche construction, phylogenetic diversity, plant-plant interactions, species assemblages, stress gradient.

Abbreviations:

RII = Relative Interaction Index (effect of the interaction on richness and abundance) (Armas et al., 2004).

Introduction

The impact of species interactions on diversity patterns has been addressed in detail in stressful environments such as the alpine belt (Cavieres et al., 2014; Liczner and Lortie, 2014; Reid et al., 2010). In alpine environments, facilitator species -often cushions and small shrubs-, alter microhabitats by buffering temperature extremes and wind, maintaining soil humidity and nutrient availability higher than open areas (Anthelme et al., 2014; Cavieres et al., 2005; Körner, 2003). The modulating effects of facilitator species under stressful environments are critical for the persistence of subordinate species outside of their optimal range and contribute to higher community richness (Badano and Cavieres, 2006; Schöb et al., 2012). This positive effect of facilitator species changes with abiotic conditions, usually turning from positive to negative between harsh and mild environments (Callaway et al., 2002). In addition, ontogeny of facilitator species (Armas and Pugnaire, 2005; Soliveres et al., 2010), soil organisms (Rodríguez-Echeverría et al., 2013; Rodríguez-Echeverría and Traveset, 2015; Van der Putten, 2009) and different morphologies within and among species may also affect the outcome of facilitator-beneficiary interactions (Bråthen and Ravolainen, 2015; Michalet et al., 2011; Schöb et al., 2012). For example, canopy morphologies among facilitator species vary widely from very compact to loose (Aubert et al., 2014), a fact which may influence microhabitat in different ways leading to facilitation. Thus, the co-occurrence of disparate facilitator species may fill a larger niche space and create higher environmental heterogeneity than a single facilitator species, increasing species richness at the whole community level.

Plant morphology is not an easy metric to use due to the complex variety of traits involved; alternatively, a useful approach to account for species similarity is to use phylogenetic relationships (Ackerly, 1997; Cavender-Bares et al., 2009). Under the

phylogenetic limiting similarity concept (Darwin, 1859; MacArthur and Levins, 1967), functional traits shaping a phenotype are considered conserved along phylogenetic lineages (Blomberg et al., 2003; but see Mayfield and Levine, 2010) including those influencing species interactions (Violle et al., 2011). Given that species sharing traits within close phylogenetic linages may have similar responses to the environment, severe environmental conditions are likely to sort species out, leading to communities with low species richness and low phylogenetic diversity (Cavender-Bares and Reich, 2012; Soliveres et al., 2012). However, and due to the effect of facilitator species in buffering extreme conditions, facilitators increase species richness and phylogenetic diversity (Butterfield et al., 2013). Thus, diversity patterns would depend, would both depend on, on environmental severity, and on the effects of facilitator species (Pistón et al., 2015; Valiente-Banuet and Verdú, 2013).

Since different shrub and cushion species create different microhabitats which could be colonized by different species (Díaz and Cabido 2001), the co-occurrence of several facilitator species would likely increase community-level diversity. However this issue has hardly been addressed (Amat et al., 2015; Zhang et al., 2011). Most reports on positive interactions concerned only one facilitator species per community, even though communities in stressful environments often include different potential facilitator species (Pugnaire et al., 2004) creating microhabitats that fulfill niche requirements of a greater variety of subordinate species. We assume that different shrubs exert net positive (i.e., facilitation) or negative (i.e., competition) effects on subordinate communities, and that the effects of different shrub species are not redundant; i.e., there is a whole range of species-specific effects of shrubs on subordinate plant communities. However, the combined effects of different, non-

109 redundant shrub species would be different, in terms of subordinate species diversity,
110 from that of individual shrub species.

111 Our goal in this study was to analyze the effects of several potential facilitator
112 species with contrasting morphologies on subordinate plant communities along an
113 environmental gradient spanning the North and South aspects in a dry mountain
114 ecosystem, linking such effects to microhabitat conditions under the canopy of each
115 shrub species. We were also interested in analyzing the contribution of co-occurring
116 shrub species to community-level species richness and phylogenetic diversity, and
117 whether the effects of facilitator species differed along the gradient. For this purpose we
118 selected in the Sierra Nevada Mountains, Spain, an environmental gradient
119 characterized by changes in temperature, water availability, and soil organic matter
120 (Sánchez-Marañón et al. 2002; Schöb et al. 2013), and recorded plant community
121 composition beneath seven shrub species and in adjacent open areas in 6 sites at
122 different elevations; three sites were in the northern aspect and three in the southern
123 aspect of the Sierra Nevada range. We expected that community composition would
124 change depending on shrub identity, being related to microclimatic conditions beneath
125 them. We expected species-specific effects of different shrubs on subordinate plant
126 communities (i.e., not only affecting intensity and sign of the interaction, but also
127 presence/absence of subordinate species and abundance). We also expected a general
128 trend in the magnitude of effects along the gradient, so that individual shrubs would
129 mostly have overall positive effects on plant community richness and plant abundance
130 under relatively harsher environmental conditions while the net effect of shrubs would
131 be neutral or competitive under milder environmental conditions, as predicted by the
132 stress gradient hypothesis (Bertness & Callaway 1994). At the community level we
133 expected a net positive effect of the whole shrub community on subordinate

134 community-level richness and phylogenetic diversity in stressful sites and no effects in
135 relatively milder sites, where negative and positive effects on subordinate species would
136 be levelled.
137
138 ## Methods
139 ### Field sites, species and data collection
140 The field sites are located in the Sierra Nevada Mountains, Southeastern Spain. We
141 selected three sites, each ca. 1 ha, on the northern aspect of the Veleta peak at 2315 m,
142 2720 m and 3240 m elevation, and three on the southern aspect of the Mulhacen peak at
143 2040 m, 2570 m, and 2900 m elevation. Both peaks are separated by a distance of 30
144 km approx. The bedrock is mica-schist, and determines the rounded and gentle hillside
145 landscape (Delgado, 2001).
146 Climate is dry continental Mediterranean with a hot and dry summer with means
147 of 17 ºC and 5 mm rainfall in July and -2.5 ºC and 90 mm rainfall in January
148 (Pradollano (37º05' N 03º23' W); 2500 m elevation;
149 http://pendientedemigracion.ucm.es/info/cif/station/es-prad2.htm). Mean annual
150 temperature decreases about 0.61 °C/100 m at the North aspect and 0.59 ºC/100 m at the
151 South aspect; mean annual precipitation increases around 30 mm/100 m at the North
152 aspect and 28 mm/100 m at the South aspect (Delgado et al., 1988). Abiotic factors
153 change with elevation, resulting in a crossed gradient where temperature and soil
154 organic matter decrease with elevation while precipitation --and soil water-- increase
155 with elevation (Pugnaire et al., 2015a; Schöb et al., 2013) as in other dry mountains
156 (Pugnaire et al., 2015b).
157 Plant communities in Sierra Nevada are characterized by a great diversity of
158 species with a high level of endemism (Delgado, 2001). Subalpine-alpine shrubland

159 communities ("piornales-enebrales") are dominated by prostrate shrubs like *Cytisus*
160 *galianoi* Talavera & P. E. Gibbs. (Fabaceae), *Genista versicolor* Boiss. (Fabaceae) or
161 *Hormathophylla spinosa* (L.) P. Küpfer (Brassicaceae), and cushion-forming species
162 like *Arenaria tetraquetra* ssp. *amabilis* (Bory) H. Lindb. fil. (Caryophyllaceae). Our
163 analyses focused on seven species that dominated plant communities at our field sites,
164 *A. tetraquetra* ssp. *amabilis*, *Bupleurum spinosum* Gouan (Apiaceae), *C. galianoi*, *G.*
165 *versicolor*, *H. spinosa*, *Juniperus communis* ssp. *nana* Syme (Cupressaceae), and
166 *Plantago holosteum* Scop. (Plantaginaceae). For simplicity we will refer to them as
167 shrubs, although two of them, *A. tetraquetra* and *P. holosteum* are cushions. Regarding
168 their morphology, and following the description of different canopy shapes by Aubert et
169 al. (2014), *A. tetraquetra* shows a semi compact creeping canopy, *B. spinosum* and *H.*
170 *spinosa* are thorny compact shrubs, *C. galianoi* and *G. versicolor* are radial hollow
171 hemispherical shrubs, *J. communis* is a thorny-prostrated shrubs and, *P. holosteum* is a
172 tufted compact cushion. Shrubs and surrounding open areas were colonized by
173 predominantly small perennial herbs and grasses (see Table S1 in Supporting
174 Information for a list with the number of species that were shrub-dependent and Table
175 S2 for the full list of species present at the sites).

176 In July 2010, at the peak of the growing season, we selected 30 individuals of
177 each of the dominant shrub species present at each site and did a paired sampling
178 beneath them and randomly in nearby open areas (but at least 1 m away the shrub
179 canopy); we recorded the number of all plant species and the their number of
180 individuals (number of shoots in the case of clonal species). For small cushions such as
181 *A. tetraquetra* ssp. *amabilis* (mean ± 1 SE; 209 cm^2 ± 12 cm^2) and *P. holosteum* (190
182 cm^2 ± 19 cm^2) the sampling was done for the whole cushion canopy and paired with
183 open plots of equal size (Schamp et al., 2013). For *B. spinosum* (4,992 ± 506 cm^2), *C.*

184 *galianoi* (8,689 ± 684 cm^2) and *G. versicolor* (10,641 ± 834 cm^2) we randomly placed
185 one 625 cm^2 quadrat per canopy paired with a similar area in the open. As *G. versicolor*
186 was larger at the low North site, we used 1250 cm^2 quadrats. For *J. communis* ssp. *nana*
187 (115,582 ± 9,340 cm^2) we sampled five randomly placed 625 cm^2 quadrats per shrub
188 and an equal number of open area plots. For *H. spinosa* (1,573 ± 101 cm^2) we sampled
189 the whole canopy area and a 625 cm^2 quadrat in open areas.
190
191 **Micro-environmental conditions along the gradient**
192 We recorded air temperature and relative humidity (RH) at hourly intervals with
193 iButtons (Maxim Integrated Products, Sunnyvale CA, USA). At each site three
194 temperature sensors were randomly placed in the open and three into the canopy, in the
195 mid-point between the stem and the edge of the canopy, of *B. spinosum, C. galianoi*, *G.*
196 *versicolor*, *H. spinosa* and *J. communis* when the species were present. Sensors were
197 placed 5 cm above ground and protected from direct solar radiation with a wooden cube
198 placed above the sensor allowing free airflow near the sensor. Using hourly values, we
199 calculated the mean air temperature and RH for August 2010 (peak of the growing
200 season at Sierra Nevada) and checked for differences between aspects (North and
201 South), elevation (low, middle and high) and microhabitat (cushion *vs.* open areas) with
202 a three-way factorial ANOVA. Temperature data were transformed with a power of two
203 to meet the homogeneity of variances and normality assumptions. Post-hoc differences
204 along the gradient were examined with Fisher's LSD tests and significant differences
205 among shrub species at each site were tested by separate contrasts within each site.
206
207 **Sign and intensity of plant interactions**

To test whether and which shrub species had positive effects on species richness and overall plant abundance (i.e., total number of individuals irrespective of the species) along the environmental gradient we measured the interaction outcome between each shrub species and the subordinate community at each site. Since there were no observable spatial distribution patterns and the substrate was homogenous, we assumed no microsite effects other than caused by shrubs. In addition, it is unlikely that hidden microsites would select rare rather than common species under nurses (Soliveres et al., 2015). Interaction outcome was measured as the relative change in species number and abundance beneath shrubs compared to open areas. We used the Relative Interaction Index (Armas et al., 2004) as $RII = (S_{shrub} - S_{open})/(S_{shrub} + S_{open})$, where S_{shrub} and S_{open} are the values of species richness and plant abundance of the subordinate community measured in the presence and absence of a dominant shrub. This index is positive when species richness or plant abundance is higher beneath shrubs than in open areas and negative when species richness or plant abundance is higher in open areas than below shrubs. Values of RII not differing from zero suggest that species richness and plant abundance are equal underneath shrubs and in open areas. We calculated the mean value of RII per site and shrub species and tested for differences among sites and among shrub species with general linear models. As our model was unbalanced and incomplete (not all shrub species were present at all sites), we re-parametrized the model using a single fixed factor with 18 "Site_Species" levels. We performed one-sample *t*-tests to check whether RII values within each site and cushion species were different from zero (i.e., neutral interaction). We excluded *H. spinosa* from all these analyses due to the differences in sampling areas between the shrub and its paired open areas.

Assessing species diversity along the environmental gradient

We tested for differences in community composition analyzing plant density (number of individuals of each subordinate species per cm^2) of all subordinate species associated to each shrub species and at each elevation by performing a Principal Coordinates Analysis (PCoA). For this analysis, we excluded subordinate species with a frequency below 5% in order to avoid rare species effects. We used Bray-Curtis distances and extracted 3 axes, which explained a total of 43% of the variance. To test if differences in community composition among shrub species were significant we used a multivariate mean comparisons test (gDGC test) based on cluster analysis, using a diagonal covariance matrix with a single linkage and a Monte Carlo simulation with 500 permutations (Valdano and Di Rienzo, 2007). We used plant density instead of abundance or composition because, given differences in plot size of different shrubs, the latter could be prone to plot-size effects while density would be less affected. Finally, to test the relationship between microhabitats (temperature and RH along the environmental gradient) and community composition (the site scores for axis 1, 2 and 3 extracted from PCoA analysis) we calculated Spearman's rank correlation (r_s).

Community level species richness and phylogenetic diversity

We assembled a phylogenetic tree with the 86 sampled species using Phylomatic3 (http://phylodiversity.net/phylomatic/). All families in our database matched family names of the angiosperm megatree (R20120829), based on the Angiosperm Phylogeny Group (Stevens 2001). Branch lengths were adjusted with the Bladj algorithm taking age estimates for the main nodes from Wikstrom *et al*. (2001) and distributing undated nodes evenly among nodes of known age as implemented in Phylocom 4.2 (http://phylodiversity.net/phylocom/).

To quantify the effect of all shrubs on community-level species richness and phylogenetic diversity we used rarefaction curves that allowed accounting for differences in sampling effort (i.e., different plot sizes) among microhabitats (i.e., shrubs and open areas). With community-level we refer to the whole community at each of the sites (i.e., all the species including all shrubs and species in open areas). In the case of species richness, we used the function *specaccum* with the rarefaction method (Oksanen et al., 2013) which finds the expected number of subordinate species by re-sampling at random the pool of shrub and open samples, plotting the average number of species for a pre-determined number of shrub and open samples (Gotelli and Colwell, 2001). For phylogenetic diversity, the total branch length of a phylogenetic tree, we used the function *phylocurve* (http://davidnipperess.blogspot.com.es/), which generates an individual-based rarefaction curve. It calculates expected phylogenetic diversity for a number of individuals per branch and per sample, and using sampling without replacement (Nipperess and Matsen, 2013). These two measurements provide different information, as species richness considers species as equally distinct from one another while phylogenetic diversity considers how much evolutionary history is behind the species in a community (Faith, 1992). Phylogenetic diversity represents individuals by their relative branch lengths without the need to establish absolute species identity (Nipperess and Matsen, 2013). Thus, different shrubs can increase species richness to a similar extent but may differ in the composition of species they host and thus in their effects on the phylogenetic diversity of subordinate communities (i.e., if two shrub species equally increased the number of species compared to open areas but species within one of the shrub species were closer in the phylogenetic tree than species within the other shrub, then the rarefaction curves for *richness* will be equal for the two shrub species but those for *phylogenetic diversity* will be quite different). To evaluate the

effect of shrubs on species diversity or phylogenetic diversity we calculated two rarefaction curves per site for each variable; one including open areas only and one taking into account all shrubs along with open areas, and plotted them for each site. All statistical analyses were conducted in InfoStat v. 2014 (Di Rienzo et al., 2014) and R 3.0.2 (http://www.r-project.org/).

Results

Mean temperature in summer was higher in the southern than in the northern aspect, decreasing by 6.2 ± 1.8ºC (mean ± 1SE) and 5.3 ± 1.5ºC from low to high elevation sites in the North and South aspects, respectively. Mean temperature beneath shrubs was 1 ± 0.3 ºC and 1.6 ± 0.4 ºC lower than in open areas in the North and South aspects, respectively. All along the gradients, temperatures were higher in open areas than beneath shrubs, except in the highest sites where temperatures did not differ (13.7 ± 0.4ºC vs. 13.5 ± 0.4ºC for shrubs and open areas, respectively, in the North, and 16.3 ± 0.2ºC vs. 16.8 ± 0.5ºC in the South). The most important effect of shrubs on temperature were at the low South site where the differences between shrubs and open areas ranged 1.3-2.5ºC (Fig. 1a, and Tables S3 and S4 for statistical results).

Mean relative humidity in summer increased with elevation by 4.2 ± 1.6% in the North, and decreased with elevation by 2.0 ± 1.0% in the South aspect. Mean relative humidity beneath the shrubs was 7.5 ± 2.9% and 8.3 ± 2.4% higher than in open areas in the North and South aspects, respectively. Moreover, relative humidity was always higher beneath shrub species than in open areas all along the gradient except for *H. spinosa* at middle sites in both aspects. The most important effect on relative humidity by shrubs were found at the low South site, where values ranged 6.9-14.9% (Fig. 1b and Table S3 and S4 for statistical results).

307 The net effect of shrubs (RII) on plant abundance (i.e., total number of
308 individuals) and species richness changed in intensity and sign depending on shrub
309 identity and environmental conditions. In general, we found positive and neutral effects
310 at the most severe sites (i.e., highest and lowest elevations in both aspects), yet one
311 shrub species (*J. communis*) always had negative effects irrespective of environmental
312 harshness. We found neutral to negative effects at milder environments (Middle sites;
313 Fig. 2). In general, *A. tetraquetra* and *C. galianoi* had positive effects under harsher
314 conditions and showed neutral or weak positive effects in milder environments. By
315 contrast, *G. versicolor* and *P. holosteum* showed consistent neutral interactions at all
316 sites where the species occurred.
317 Community composition of subordinate species (i.e., number of individuals per
318 species and cm^2) differed among shrub species as shown by PCoA analysis (Fig. 3a)
319 and post-hoc gDGC tests (Fig. 3b). It was significantly different under the different
320 shrub species within a site, with some exceptions (e.g., *C. galianoi* and *H. spinosa* at the
321 low South site; *C. galianoi* and *G. versicolor* at the middle South site, and *H. spinosa*
322 and *J. communis* at the high South site). However, this data could be prone to plot size
323 effects and thus should be taken with caution. The number of dependent subordinate
324 species (i.e., species found only under shrubs) ranged from 1 under *P. holosteum* at the
325 middle North site up to 13 under *C. galianoi* at the low South site (Table S1).
326 Subordinate communities changed with microhabitat conditions along the gradient.
327 Axis 3 extracted from the PCoA analysis positively correlated with RH; however, axes
328 1 and 2 from the PCoA did not correlate with any of the abiotic factors measured (i.e.,
329 temperature or RH, Table 1).
330 Shrubs increased community-level species richness (Fig. 4) at the most
331 environmentally extreme sites of the gradient (i.e., low and high sites in both aspects).

The highest contribution was recorded at the warmest site (the low South site) (Fig. 4f and 5f) with the highest differences in abiotic conditions (temperature and RH) beneath shrubs *vs.* open areas (Fig. 1). At this site, *C. galianoi* showed strong positive effects on the subordinate plant community whereas other shrub species had neutral effects (Fig. 3). Furthermore, shrubs increased community-level phylogenetic diversity at all sites (Fig. 5). The effect was stronger at the middle and low North and at the highest South where community-level phylogenetic diversity increased due to the presence of the shrubs species by 146,562 Myr, 154,003 Myr and 153,801 Myr, respectively.

Discussion

As a whole, shrub buffered harsh abiotic conditions by decreasing summer temperatures and increasing RH in their understories with respect to open areas along the gradient. Subordinate communities differed not only across shrub species but also across sites, although occasionally different shrub species hosted similar communities within a site. Such differences in subordinate community composition were mostly related to microhabitat conditions created by shrubs (i.e., water balance), suggesting a dependence of beneficiary species on their facilitators. The effects of shrubs on overall plant abundance and species richness differed with shrub identity and elevation. In sites where abiotic conditions were most extreme (i.e., high North due to low temperatures or low South due to high temperatures and low relative humidity), the combined effect of shrubs on subordinate species richness increased whole-community richness compared to open areas. This effect was evident when at least one shrub species showed positive effects on species richness and abundance compared to open areas. Interestingly, shrubs increased community phylogenetic diversity at all sites.

Differences in microhabitat conditions

Shrubs can modify the microhabitat beneath their canopies influencing growth and survival of beneficiary species (Anthelme et al., 2014; Brooker and Callaway, 2009; Cavieres and Badano, 2009; Pugnaire et al., 2015a; Pugnaire et al., 2015b). For example, they can buffer temperature extremes under their canopies reducing summer heat shock, transpiration, and soil water evaporation and reducing winter frost damage (Körner, 2003). In our case not all shrub species within a site changed their microhabitat in the same way during the growing season, suggesting that species with different canopy morphology created different microhabitats with contrasting effects on communities of subordinate species. Molina-Montenegro et al. (2006) showed significant differences between microhabitat conditions of two cushion species (*Azorella monantha* and *Laretia acaulis*) in an alpine zone of Central Chile but they did not evaluate their effects on subordinate plant communities, and most studies performed in alpine systems that measured more than one cushion species did not distinguish the different effects of cushions on microhabitat conditions (Cavieres et al., 2007; Chu et al., 2009; Wang et al., 2008).

Shrub effects on subordinate species richness and abundance

Usually there is a range of net positive to net negative effects among species in plant communities (Callaway et al., 1991; Holzapfel and Mahall, 1999; Maestre et al., 2003; Pugnaire et al., 2004; Wang et al., 2008). Moreover, plant interaction intensity and sign are expected to change along environmental gradients depending on abiotic conditions so that net positive interactions would prevail at the most severe part of the gradient while net negative interactions would prevail at the milder part, as predicted by the stress gradient hypothesis (SGH; Bertness and Callaway, 1994). Indeed, we found that

382 at sites where abiotic conditions were most extreme, and at least one shrub species had
383 positive effects, there was an increase of community-level species richness and
384 phylogenetic diversity. This was also the case along the North aspect of the Sierra
385 Nevada mountains, where Pistón et al. (2015) found that the effect of nurses on closely
386 related species varied from positive to negative as the environment became less severe
387 while on more distantly-related species it remained neutral. These, and our own results,
388 support the role of facilitation in expanding the distribution range of beneficiary species
389 (Armas et al., 2011; Butterfield et al., 2013; Pugnaire et al., 2015b; Valiente-Banuet and
390 Verdú, 2013).

391 Shrubs showing positive effects on plant species richness and abundance under
392 harsh conditions changed their effect to neutral under milder conditions (i.e. *A.*
393 *tetraquetra* at both middle sites and *C. galianoi* at the middle South site), while shrubs
394 that always showed neutral or negative effects on plant diversity along the gradient,
395 never had positive effects (i.e., they were always non-facilitator species irrespective of
396 environmental conditions; *B. spinosum*, *G. versicolor, J. communis* and *P. holosteum*).
397 In severe environments plant interactions rely on morphological and physiological
398 traits, which have many species-specific consequences (Armas and Pugnaire, 2011;
399 Aubert et al., 2014; Schöb et al., 2013). Thus, two shrub species may have similar
400 canopy morphology but one may have negative effects on subordinate species, i.e.,
401 allelopathic effects, such as *J. communis* in our field sites (Castro et al., 2005), whereas
402 other shrubs may host symbionts (e.g., N-fixing bacteria, such as *C. galianoi*), plant
403 growth-promoting bacteria or mycorrhizae that would positively affect the subordinate
404 community (Martínez, 2009; Martínez-García and Pugnaire, 2011; Rodríguez-
405 Echeverría et al., 2013). Therefore, niches created by coexisting shrub species may be

406 similar but rarely identical, and these species-specific differences could influence
407 subordinate plant communities.
408
409 **Differences in subordinate community composition among shrub species**
410 Communities of subordinate species differed among shrub species along the gradient,
411 with few exceptions. Although shrub species may appear functionally redundant under
412 certain environmental conditions, the microhabitats they create could actually differ.
413 For example, *C. galianoi* and *G. versicolor* share similar morphology but the
414 microclimate beneath their canopies was vastly different, hosting different communities
415 of subordinate species. Overall, shrubs had net positive effects in our sites, which means
416 that assemblages of shrub species could fill larger niche spaces and create more
417 environmental heterogeneity (Harper, 1977; Jones et al., 1994) than a single species.
418 Kikvidze et al. (2015) found, however, that niche space constructed by cushion species
419 was more homogeneous than that in open areas. In any case, the combined effects of
420 shrub species in a community deeply influence whole-community species richness,
421 phylogenetic diversity and ecosystem function (Cadotte, 2013; Loreau et al., 2001).
422
423 **Context-dependence of co-occurring shrub species effects on community diversity**
424 The increase in community-level species richness due to the presence of different shrub
425 species was parallel to an increase in phylogenetic diversity except at the middle sites.
426 The highest contribution of shrubs to whole-community species richness was found at
427 the low South site, where the facilitative effect of *C. galianoi* on subordinate species
428 was strongest. In this site, the net effect of the different shrub species on richness was
429 positive although among individual shrub species there were simultaneous neutral and
430 positive effects. Furthermore, the combined effects of all shrub species increased

phylogenetic diversity at all sites along the environmental gradient. Previous studies showed that cushions create phylogenetically unique communities relative to open areas in severe environments (Butterfield et al., 2013; Pistón et al., 2015). Our results suggest that species richness and phylogenetic diversity responded differently to the dominant shrub species.

As environmental severity decreased towards middle sites, whole-community species richness was similar to that of open areas. This result suggest that coexistence was stable at these sites following the spatial storage effect; this mechanism is the most feasible in a heterogeneous environment, enabling coexistence by buffering population growth rates (also called "source-sink dynamics"; Dias, 1996). This mechanism prevents the exclusion of species inhabiting the whole community (Amarasekare, 2003; Sears and Chesson, 2007). Therefore, shrubs could act as source habitat for some species (i.e., those more abundant within shrubs than in open areas) and as sinks for species that dominate open habitats (i.e., those less abundant under shrubs than in the open areas). In some places e.g., the highest site in the South aspect, open areas could be acting as sinks and the understories of *A. tetraquetra* and *C. galianoi* as sources. However, to verify the presence of such source-sink dynamics in our system we would need to quantify the *per capita* growth rates of each subordinate species (Dias, 1996), which we did not. Nevertheless, just comparing the number of dependent subordinate species on specific shrubs could be indicative of such processes. For example, 13 shrub-dependent species were found under *C. galianoi* at the low South site, and 8 species were found under *G. versicolor* in the low North site (Table S1). These are clear indication that shrubs may act as a source habitat for these species at a specific site and that spatial storage effects could indeed be quite relevant in our study system.

Conclusions

Our study showed the importance of the combined effect of co-occurring shrubs on species richness and phylogenetic diversity at the community level, despite individual shrub effects ranging from positive to negative. These differences in species-specifics effects are most likely due to the creation of different niche spaces which allow stress-sensitive species to survive in environments otherwise too harsh for them. Thus, the effect of different shrub species on plant community richness and phylogenetic diversity is not redundant as they host unique communities, particularly under harsh environmental conditions. This highlights the importance of conserving the variety of co-occurring shrub species, as their net effects on community diversity may be critical to maintain biodiversity and ecosystem functions in this fragile ecosystem.

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673 **Appendix A. Supplementary data**

674 Supplementary data associated with this article can be found, in the online version, at

675 XXX

	Temperature			RH	
	n	r_s	*p*-value	r_s	p-value
Axis 1	16	0.18	0.49	-0.08	0.76
Axis 2	16	-0.06	0.83	0.38	0.15
Axis 3	16	0.33	0.21	**0.49**	**0.05**

Table 1. Spearman correlation (r_s) of mean temperature and mean relative humidity (RH) beneath shrubs and community composition (site scores extracted from axis 1, axis 2 and 3 of the PCoA analysis of subordinate plant density for each shrub species at each site; Fig. 3a). *n* is the total number of microhabitats along a severity gradient with environmental data, and *p*-value is the significance test of the correlation analysis. Significant results are shown in bold.

710 **Figure 1.** Mean temperature and relative humidity (RH) of air beneath shrub species
711 and open areas along two elevational gradients in Sierra Nevada, Spain. Values are
712 means ± 1SE (n = 3). L = Low elevation; M = Middle elevation; H = High elevation; Bs
713 = *Bupleurum spinosum*; Cg = *Cytisus galianoi*; Gv = *Genista versicolor*; Hs =
714 *Hormathophylla spinosa*; Jc = *Juniperus communis* ssp. *nana*; Op = open microhabitats.
715 Asterisks indicate the results of contrasts between each shrub species compared to open
716 areas at each site: a = $p < 0.05$, b = $p < 0.01$, c = $p < 0.001$ and ^{ns} not significant results.
717
718 **Figure 2.** Relative interaction index (RII) showing every shrub effect on abundance
719 (i.e., total number of individuals over all species) (a) and on species richness (b) of
720 subordinate communities along the elevation gradient (n = 30). Data are means ± 1SE.
721 L = Low elevation; M = Middle elevation; H = High elevation; At = *Arenaria*
722 *tetraquetra* ssp. *amabilis*; Bs = *Bupleurum spinosum*; Cg = *Cytisus galianoi*; Gv =
723 *Genista versicolor*; Hs = *Hormathophylla spinosa*; Jg = *Juniperus communis* ssp. *nana*.
724 Symbols with an asterisk represent RII values significantly different from 0; *$p < 0.05$,
725 **$p < 0.01$, ***$p < 0.001$. The "site_shrub species" factor was significant ($p < 0.001$)
726 for both RII measures.
727
728 **Figure 3.** Differences in subordinate species composition (individuals per species and
729 cm^2) among sites and shrubs. Species with a frequency less than 5% were excluded (a)
730 (n = 59). Multivariate mean comparisons (gDGCtest) testing differences in plant
731 densities among shrubs along elevational gradients at the Northern and Southern aspects
732 of the Sierra Nevada mountains based on cluster analysis. We used a diagonal
733 covariance matrix with a single linkage and Monte Carlo simulation with 500
734 permutations. The direction of the arrow indicates significant differences in the

735 subordinate plant species density ($p < 0.05$) among each shrub (b). North aspect low in
736 blue; North middle in orange; North high in red; South aspect low in green; South
737 middle in black; South high in magenta. At: *Arenaria tetraquetra* ssp. *amabilis*; Bs:
738 *Bupleurum spinosum*; Cg: *Cytisus galianoi*; Gv: *Genista versicolor*; Hs:
739 *Hormathophylla spinosa*; Jc: *Juniperus communis* ssp. *nana*; Ph: *Plantago holosteum*.
740
741 **Figure 4.** Shrub contribution to community species richness at each site. (a) HN:
742 Northern aspect high with two shrub species; (b) MN: Northern middle with four shrub
743 species; (c) LN: Northern low with five shrub species; (d) HS: Southern aspect high
744 with five shrub species; (e) MS: Southern middle with four shrub species; (f) LS:
745 Southern low with four shrub species. Values are mean ± SD. Significant differences
746 are indicated by non-overlapping error terms of the curves at the asymptote.
747
748 **Figure 5.** Shrub contribution to community phylogenetic diversity (total branch length
749 of the tree in Myr) for each site. (a) HN: Northern aspect high with two shrub species;
750 (b) MN: Northern middle with four shrub species; (c) LN: Northern low with five shrub
751 species; (d) HS: Southern aspect high with five shrub species; (e) MS: Southern middle
752 with four shrub species; (f) LS: Southern low with four shrub species. Displayed are
753 means.
754

Figure 1

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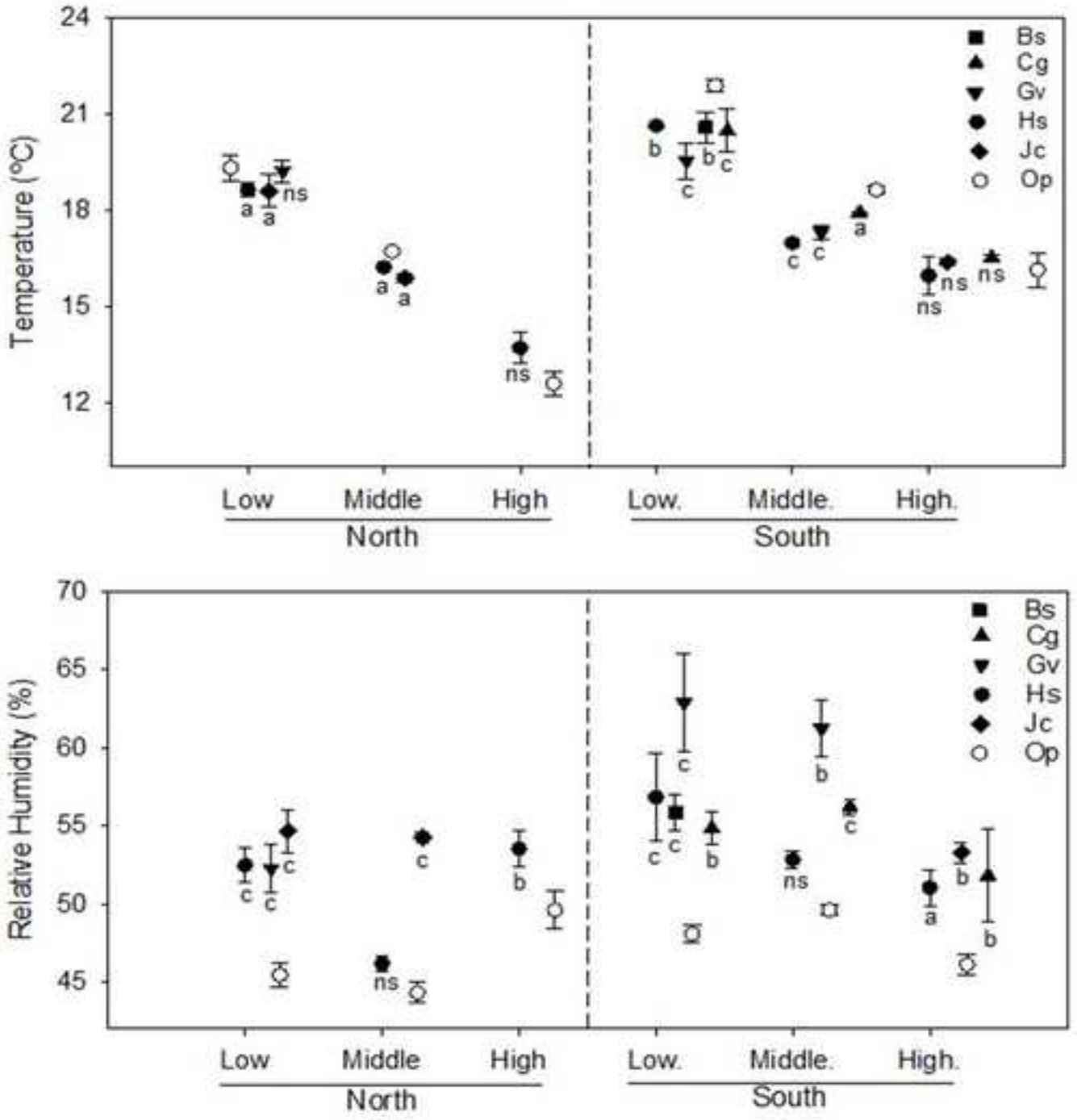

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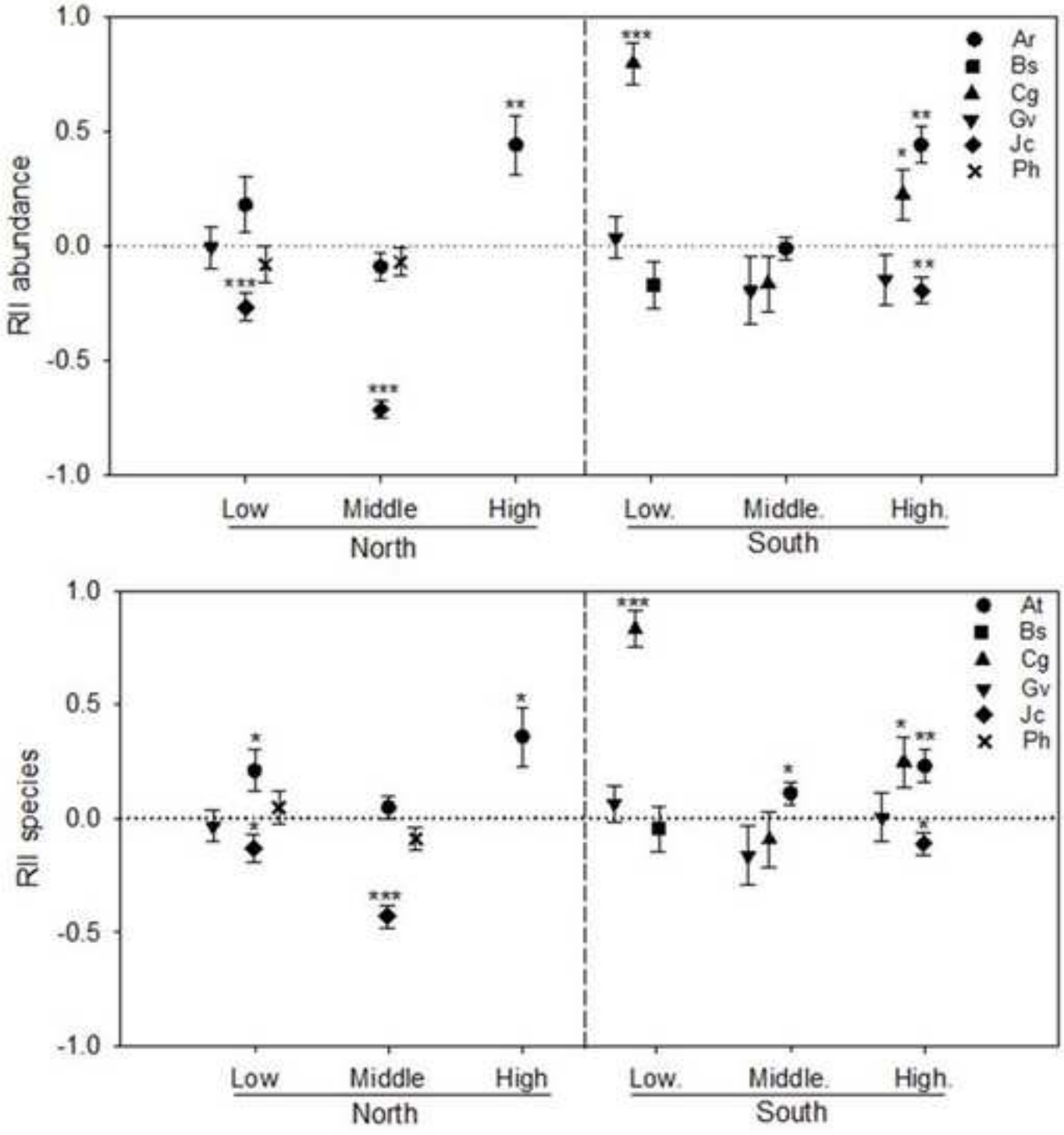

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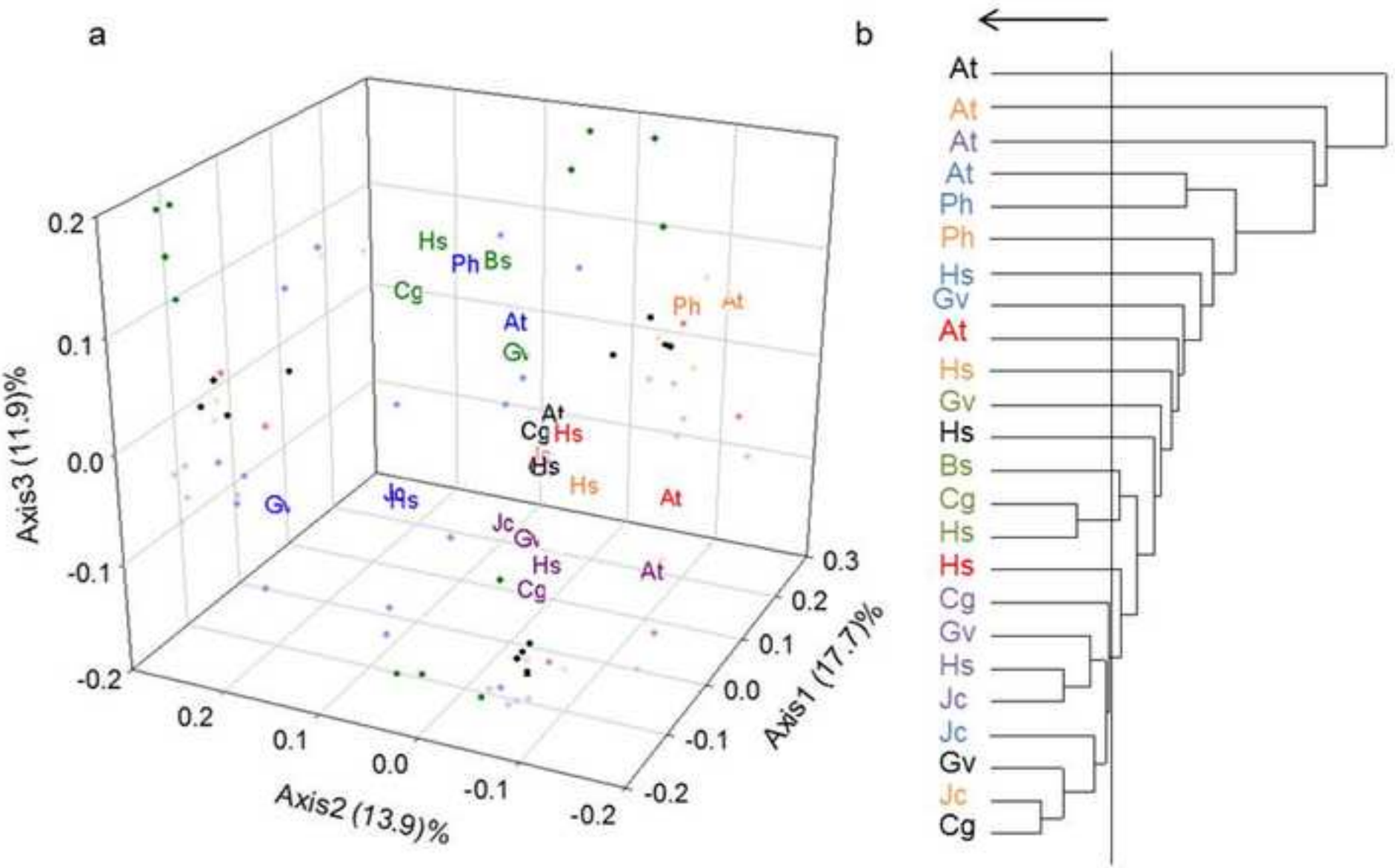

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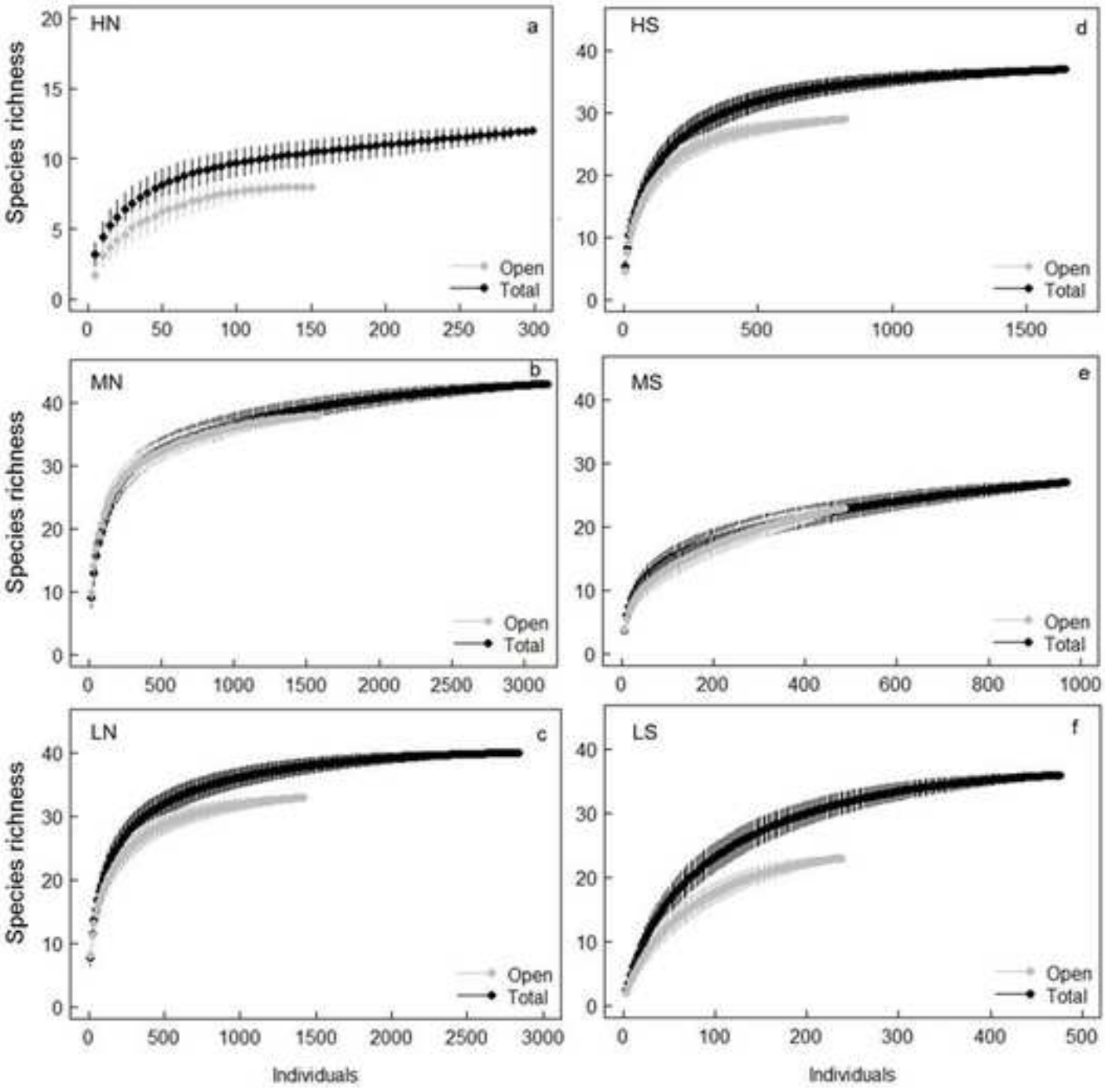

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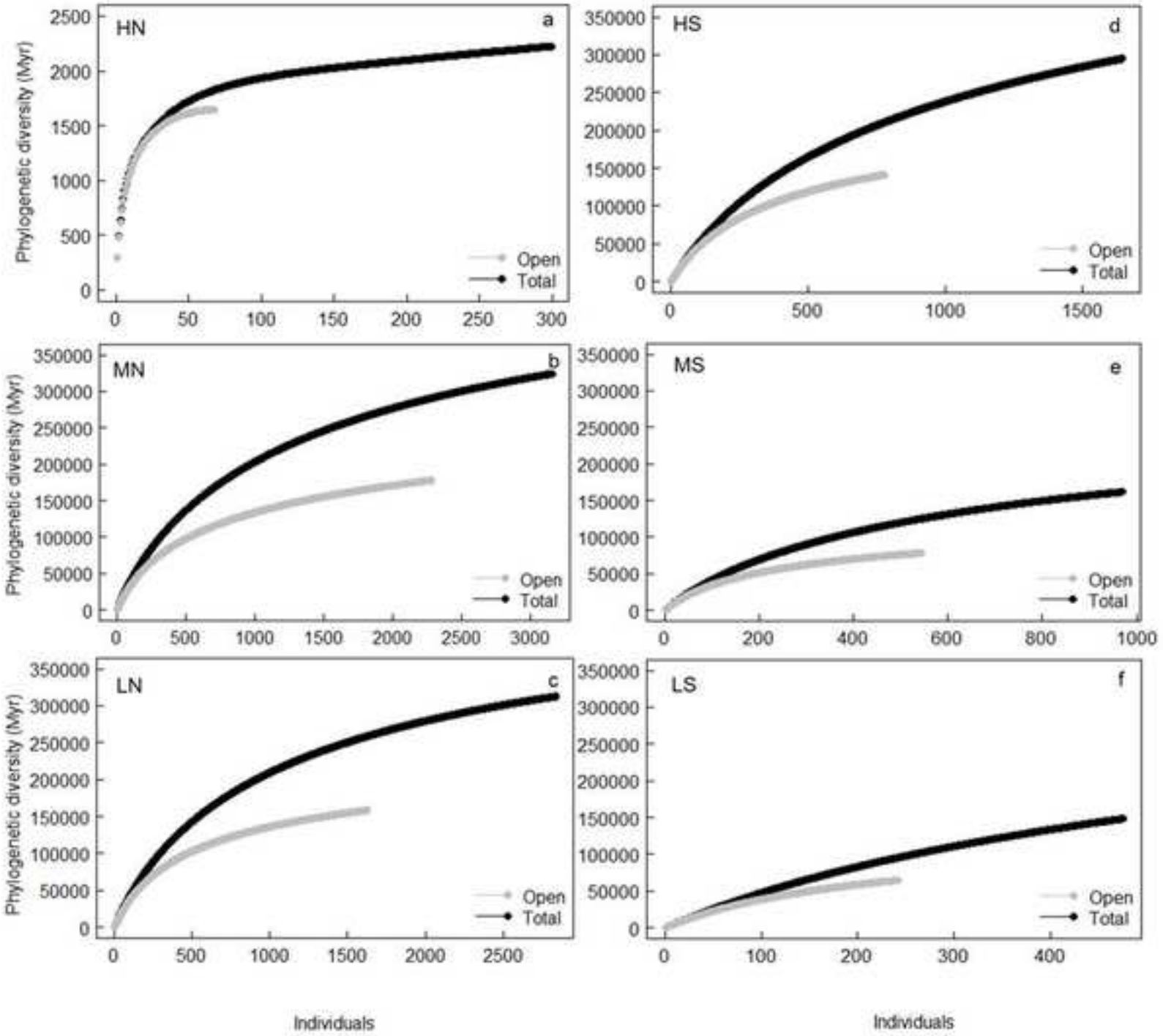

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